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The importance of migration to the butterfly fauna of Arabia
(Lep., Rhopalocera)

by
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Introduction

Some years ago I published an account of the migrant butterflies of Lebanon, East Jordan and Egypt (LARSEN, 1976). The main conclusions were that 1) migration was an important element of the total fauna, 2) that migration was not a regular and relatively predictable north/south movement, such as it may appear to an observer in northern Europe, and 3) that the proportion of migrant species in the total fauna increased considerably as one moved towards ecological zones hostile to butterflies (table 1).

Table 1: Migrant species as a proportion of the total butterfly fauna in Lebanon, East Jordan and Lower Egypt (LARSEN, 1976)

	Lebanon	E. Jordan	Egypt
Migrant species	26	20	20
Total species	136	79	41
Percent migrant	18,7 %	25,4 %	48,8 %

On the whole such data support the theory of SOUTHWOOD (1962) that migration evolved as a response to periodically adverse climatic and ecological conditions.

The aim of this paper is to make a similar analysis of the Arabian butterfly fauna which I have been studying in detail during the past six years. The data are taken from the manuscript of a book on the butterflies of Arabia (LARSEN, in press) and from various recent papers (LARSEN, 1976, 1977a, 1980; LARSEN & LARSEN, 1980; PITCHER, 1979; PITTAWAY, 1979, 1980, 1981).

Migrant butterflies of Arabia

The migrant butterflies of Arabia fall into three rough categories which will be designated regular, moderate and weak respectively.

1) Regular migrants:
This category comprises species which regularly undertake long-distance directional movements, often in large numbers, and where migration is an essential component in their life cycle and survival strategies. Some of these species would probably rapidly become extinct in all or most of their distribution area in the absence of active migration.

Pontia daplidice LINNÉ is a well known migrant with a wide distribution in the Palaearctic. In Arabia it is found only in the mountains of southwestern Arabia and in Oman. Whether these populations are in current migratory contact with the main population is not known, but there is no suggestion of subspeciation. GABRIEL (1954) united Yemeni and Ethiopian material under ssp. aethiops de JOANNIS & VERITY but I can find no justification for such a view. My own series from both localities are quite typical.

Anaphaeis aurota FABRICIUS is distributed in India, Arabia and all of Africa, occasionally penetrating to the eastern, Mediterranean. It is one of the most frequent and persistent of all migrants, often moving in huge masses (LARSEN, 1977b). There are records from all parts of Arabia.

Anaphaeis creona CRAMER is common throughout Africa where it is one of the most frequent long distance, large scale migrants, often in company with the preceding species. In Arabia, the species is limited to wet localities in southwestern Arabia in what appears to be a valid subspecies (ssp. *leucogyne* BUTLER) which appears to have lost all or most of its migratory capacity.

Colotis (Madais) fausta OLIVIER is limited to the Indian sub-continent and parts of the Middle East, with a slight extension into parts of eastern Africa. It regularly migrates into the témperate zone in the eastern Mediterranean and Iraq/Iran where it builds up substantial populations which cannot survive winter. There are few if any areas where the species can survive on a permanent basis since summer in central parts of Arabia is too dry and hot. The species could be considered "nomadic".

Catopsilia florella FABRICIUS is found in India, Arabia and Africa where it is one of the most accomplished migrants, penetrating to the eastern Mediterranean in some years. It has been found in most parts of Arabia.

Colias crocea FOURCROY is a well known Palaearctiv migrant which in Arabia occurs under oasis conditions in eastern and central Arabia. Whether the populations can survive in Arabia on a permanent basis is not quite certain, but it seems likely that extinction takes place in exceptionally hot years.

Lampides boeticus LINNÉ is a pan-Palaeotropical migrant which on occasion penetrates deep into the Palaearctic. It has been found in most parts of Arabia, but does not appear to be all that common.

Danaus chrysippus LINNÉ is a pan-Palaeotropic migrant which penetrates the témperate zone from time to time. It has been found in all parts of Arabia and has been seen at sea in the Persian Gulf. The high frequency of the forms *dorippus* and *alcippus* in southwestern Arabia and their almost total absence from Central and eastern Arabia may indicate that gene-flow is limited and that the eastern Arabian populations have an Oriental origin.

Vanessa cardui LINNÉ is a well known almost global migrant which has been recorded all over Arabia. Dr. G. POPOV informed me that he had seen immense

numbers of larvae near Medain Salih in April 1947 in the company of locust hoppers and advancing with these as the vegetation was totally eaten.

Junonia orithya LINNÉ is a pan-Palaeotropical species which has more subspecies than is usual in migrant butterflies. Possibly the subspecies of the wet tropics do not migrate. In Arabia it occurs as ssp. *here* LANG, which is found also in neighbouring parts of Asia and occasionally in Sudan and Ethiopia. Very surprisingly a narrowly localised subspecies (ssp. *cheesmanni* RILEY) occurs in coastal parts of eastern Arabia and on Bahrain island, surrounded on all sides by migratory populations of ssp. *here*. It has maintained itself unchanged for at least 50 years.

Phalanta phalantha FABRICIUS inhabits most of the drier parts of the Old World tropics as well as some wetter areas. In the dry zone it migrates extensively. I found it in Yemen for the first time in 1980 (LARSEN, 1982); it may have been temporary colonisation. In 1981 the species was much more common that in the previous year which had received exceptionally good rains.

2) Moderate migrants:
This group includes species which have frequently been noted as long distance directional migrants but where migration does not appear to be an essential part of their life cycle and survival strategies.

Papilio demoleus LINNÉ is found throughout the Oriental region, in parts of Iran and Iraq as well as in eastern Arabia. It is a known migrant. Its arrival in Arabia must be very recent as it is totally dependent on cultivated *Citrus* under oasis conditions. Since 1956, when the species was first recorded in Iraq, it has spread to the whole of the Iraqi lowlands (LARSEN, 1977c). It has managed to colonise most oases in eastern Arabia and northern Oman where *Citrus* is cultivated.

Pieris rapae LINNÉ is a Palaearctic migrant with a wide area of distribution which has colonised parts of North America. It occasionally reaches Qatar, eastern Arabia and parts of the Nejd in central Arabia (PITTAWAY, 1979, 1980, 1981). The limited material available indicates an Iranian origin for those in eastern Arabia and a Mediterranean origin for those of central Arabia.

Colotis calais CRAMER is a widespread butterfly in Africa, southern Arabia and parts of India. There are scattered records of active migration and the species usually manages to colonise even very isolated stands of the food plant.

Colotis phisadia GODART occurs in a single subspecies from Mauretania to Oman, while there are some distinct subspecies in the Ethiopian area and in India. It is also found in the Dead Sea Valley and in the massifs of the Sahara. There are numerous firm migration records, including one from Jordan which was taking the species up the Jordan valley to areas where the food plant is no longer found (LARSEN & NAKAMURA, in press). It has been seen migrating also at sea off Aden (WILLIAMS, 1930).

Eurema hecabe LINNÉ is widespread throughout the Old World tropics and in southern Arabia from Medina to Aden and from there to Dhofar. An isolated colony was discovered in eastern Arabia (PITCHER, 1979); most probably this was imported with animal food-stuffs.

Colias erate ESPER is found in Ethiopia and Sudan in the subspecies *marnoana* ROGENHOFER which may in fact be alied to *C. poliographus* MOTSCHULSKY, if that is a good species (a suggestion kindly made by L. G. HIGGINS). It has been caught in Arabia only in 1936 when H. ST. J. PHILBY collected a few in the southern part of the Asir mountains. They may be immigrants from Africa though ecological conditions in Yemen and the Asir seem quite suitable.

Colias electo LINNÉ is very common in the high mountains of Yemen and the Asir, in montane East Africa and at lower levels in South Africa. Like many of its congeners it migrates though there are no firm records from Arabia.

Deudoryx livia KLUG is found in tropical Africa north of the Sahara, in Arabia and in the eastern Mediterranean, where it is reinforced by migrants. It cannot survive permanently in Lebanon. Its occurrence in most parts of Arabia is erratic and typical of a migrant species; it has been taken at 2000 m + in Oman at which height it almost certainly could not survive winter.

Syntarucus pirithous LINNÉ is found throughout Africa, in southwestern Arabia and in the Mediterranean from where it invades Europe. The Lebanon does not appear able to support permanent populations of this butterfly. There are direct observations of migration from Egypt (WILLIAMS, 1930, 1939).

Azanus jesous GUÉRIN is a species whose distribution pattern and periodic occurence in areas where it was not previously found indicates considerable migratory powers. It is found in all of Africa, most of Arabia and much of India; it is also found in the eastern Mediterranean where at least the Lebanon populations are probably not permanent.

Azanus ubaldus CRAMER has a pattern similar to that of the previous species, but it does not extend to Lebanon. It is occasionally recorded from Tunisia. Its occurrence in Oman is unpredictable, indicating that migration plays a part. It extends to southern Jordan, but there are few records.

Byblia acheloja WALLENGREN has been observed as a migrant in many parts of its range which covers Africa and southwestern Arabia. I have seen it in a joint migration with several other species in Benin in West Africa (LARSEN, 1978a).

Junonia hierta FABRICIUS has been recorded as a migrant in the Afrotropical and Oriental parts of its range, which includes southern Arabia (e.g. WILTSHIRE, 1948 and LARSEN, 1978a). It occasionally migrates into Lower Egypt and very rarely reaches the Lebanon (LARSEN, 1974).

Hypolimnas misippus LINNÉ is distributed throughout the Old World tropics

from where it may migrate into the Palaearctic in the eastern Mediterranean and southern Iraq. It is widespread in Arabia, but uncommon in the eastern and central parts.

Hypolimnas bolina LINNÉ is a well known Oriental migrant which has established itself in Madagascar and on the island of Socotra off Somalia, probably introduced accidentally by man when Madagascar was being colonised by peoples of East Asian origin more than 1000 years ago. A single specimen from Dhofar (LARSEN & LARSEN, 1980) must have been an immigrant from Socotra.

Pelopidas thrax HÜBNER is a migrant into the East Mediterranean but its precise status as a migrant is not well known.

3) Weak migrants:
This group comprises species which have not often been seen in typical migrations, but whose distribution patterns, relative lack of geographical differentiation and unpredictability of occurrence at the fringes of their range indicates that some degree of migration is involved which permits the immediate colonisation of suitable territory.

Papilio demodocus ESPER is widely distributed in Africa and flies in Arabia from Medina to Aden and from there to Dhofar. E.P. WILTSHIRE remembers having seen specimens from the Sinai, but does not recall the exact circumstances (pers. comm.).

Colotis chrysonome KLUG is found in dry parts of Africa north of the Equator, in the Saharan mountain massifs, in the Dead Sea Valley of Jordan and in southwestern Arabia, Dhofar and northern Oman. In Arabia there is also a record from near Riyadh where the species has not been seen in recent years though the food plant is present.

Colotis evagore KLUG is known as a migrant in Morocco, where it is regularly caught at 2000 m +, far from any breeding localities. In Arabia this African species is known only from the southwestern areas at low altitude and its migratory capacity in Arabia appears limited.

Eurema brigitta STOLL is found throughout the Old World tropics and most of the Oriental region. In Arabia it is rare and limited to southwestern Arabia. It has been noted as a migrant, but it is doubtful whether it migrates for long distances.

Deudorix antalus HOPFFER is widely distributed in Africa and pushes its distribution to the absolute limits of its ecological tolerance. In Arabia it is limited to the southwestern areas.

Acraea eponina CRAMER has been recorded as a migrant in Eritrea (JANNONE, 1948). It has been recorded only once in Arabia at high levels in the Yemen mountains (LARSEN, 1982).

Acraea encedon LINNÉ was also recorded as a migrant in Eritrea (JANNONE, 1948). It is widespread in southwestern Arabia in a fairly distinct subspecies (ssp. *rathjensi* WARNECKE).

Pelopidas mathias FABRICIUS is widely distributed in Africa and Asia and has been captured in most of Arabia. There are few definite observations of migration (e.g. WILLIAMS, 1930), but its ditribution and ecology indicates that it is in fact migratory.

Borbo borbonica BOISDUVAL is widely distributed in Africa and the Oceanic islands, occasionally penetrating to the eastern and western Mediterranean. The species is almost certainly migratory or at least able tu push its distribution to the limit of its ecological tolerance. There are a few scattered records from western Arabia.

Gegenes nostrodamus FABRICIUS has been recorded from various parts of Arabia, where it seems scarce and local. It is found in the Mediterranean basin, across Asia Minor to India. Its capacity for migration is demonstrated by the fact that it has penetrated up the Nile, at least to Kharthoum in Sudan.

Migration and passive dispersal

All the species in question are migrants in the narrow sense of the term, i.e. there is direct or imputed evidence for regular or occasional long-range, directional movement under the direct control of the insects involved. No-one who has witnessed or followed a butterfly migration can fail to have been impressed at the determination of the insects and their ability to maintain the chosen direction in spite of topography and wind. This is in contrast to passive dispersal controlled essentially by metereological conditions. Some migrant moths reaching Finland have been convincingly traced back in relation to frontal systems, showing their origin in the Russian steppes — in full accord with a priori considerations (MIKKOLA, 1967). It is well known that locusts may be transported by winds in directions totally opposed to the orientation of the millions of insects in the swarm; appararently orientation of individual insects has a bearing on swarm cohesion rather than on direction (RAINEY, 1978: figs. 2 u. 6). Due to the special meterological conditions in the inter-tropical convergence zone, most locust swarms eventually reach a desirable destination, but they have little control over this.

Most butterfly migration takes place very close to the ground, usually only a few metres, sometimes 40 or 50 metres above the surface. The direction of hundreds of flights analysed by WILLIAMS (1930) show them to be largely independent of wind direction; migrations into the wind are not unusual. Doubtless strong sidewind would result in some drift in relation to the orientation of the individuals, but not enough to constitute passive displacement. At Natitingou in Benin in West Africa I witnessed a major mixed migration which maintained the same basic direction on two subsequent days where the wind changed from sidewind from the East to due West (LARSEN, 1978a).

The fact that butterflies are able to lock themselves onto a directional path and to maintain it for some considerable time does not imply that all migratory behaviour is a manifestation of the same underlying cause. Several different phenomena appear to be involved. It is not the purpose of this paper to attempt to create a typology of migration, but a few comments may be worthwhile.

a) One group of migrants move between breeding sites and hibernation sites, usually vertically up and down mountains. This is the case for species of *Gonepteryx, Aglais urticae* LINNÉ and *Issoria lathonia* LINNÉ in Lebanon (LARSEN, 1976). Rather similar conditions appear to prevail in California (SHAPIRO, 1980). The incredible migrations of *Danaus plexippus* LINNÉ from USA and Canada to wintering sites in Mexico and California is simply and ectreme of this type of migration. It is characteristic of this group that the same individual makes the migration in both directions, as in birds. In other migrant butterflies any given individual moves in only one direction, while later movements are made by their offspring.

b) In southern India and in Sri Lanka there is more migration activity than anywhere else in the world. Many species are involved, the migrations are seasonal and very predictable in timing and direction, less so in numbers of specimens involved (WILLIAMS, 1927; LARSEN, 1978b). The most logical interpretation of such a pattern is that it has developed as an alternative to diapause, allowing the species in question to use food resources on both flanks of the mountains with different growing seasons. In the course of the migrations in the Nilgiri mountains the butterflies cross at altitudes which are too high to allow breeding by the species involved (LARSEN, 1978b). There may be somewhat similar movements also in *Eritrea* (JANNONE, 1948).

c) Some of the major migrants (e.g. *Vanessa cardui, Pontia daplidice, Madais fausta, Colias crocea, Lampides boeticus, Catopsilia florella* and *Anaphaeis aurota*) appear to be pursuing a strategy of permanent nomadism. Migration ensures that where-ever suitable breeding conditions exist, butterflies will soon arrive to exploit them. Many of the migrant species developed in arid environments where the danger of extinction is always present and migrate into areas where permanent survival is impossible. Viewed from northern Europe and especially the United Kingdom it might appear that migrant species essentially move northwards; the same is true when tropical immigrants are viewed from Lebanon and Jordan. WILTSHIRE (1946) stated that migration is best studied at source rather than at destination. When this is done, the picture is less clear. In *Vanessa cardui*, on which more data are available than for other species, there is no clear correlation between the direction of flights and season in the eastern Mediterranean, nor is it clear that any one direction is a priori better than another. In April 1947, GEORGE POPOV saw masses of *V. cardui* larvae at Medain Salih in the Saudi Arabian Hejaz, competing for food with locust hoppers and having to advance on foot as food supplies were dpleted by their joint efforts. No food

supplies would have been available when the imagines hatched. It is not clear that any given geographical direction would be the best choice for a subsequent migration. There would be potentially suitable breeding grounds to the North in Syria, Lebanon and Turkey, to the West in the Nile Valley, to the East in the Zagros, and to the South in Yemen and Ethiopia. In this group of migrants, migration is an almost essential component of their life cycle and survival stretegy, developed in place of shopisticated aestivation and hibernation mechanisms. It is interesting to note that *Pontia glauconome* KLUG, a close relative of *Pontia daplidice* specialising in desert conditions, does not migrate but can spend several years in pupal stage.

d) There are no records of *Vanessa atalanta* LINNÉ from tropical Africa or Arabia, and it reaches Egypt only infrequently. This is an indication that this species, at least, does have a northwards bias in its migration out of the Mediterranean. This is also true for *Pieris brassicae* LINNÉ.

e) Many of the species listed as weak migrants probably only migrate occasionally in response to special stimuli (e.g. overcrowding).

The importance of migration to the Arabian fauna

While the actual phenomenon of migration is probably a complex one, this is of lesser importance for the main theme of this paper. Whatever the causes of migration, the expected effects should be the same: the more hostile the environment, the larger the proportion of migrant species should be. This hypothesis clearly holds true for Arabia. In the lush mountains of Yemen (up to 2000 mm of annual rainfall) only 27 percent of all species are migratory. In the deserts and oases of central and eastern Arabia nearly 60 percent of the total are migratory. In intermediate ecological zones, the percentages are also intermediate (table 2).

Table 2: The proportion of migrant butterflies in different parts of Arabia in decreasing order of ecological suitability for butterflies

Region of Arabia	Total butterflies	Migrant species	Percent migratory
Yemen Arab Republic	121	33	27 %
Aden District	92	28	30 %
Dhofar	62	21	34 %
Oman	48	20	42 %
Asir	70	30	43 %
Central Arabia (Nejd & Nefud)	32	18	56 %
Eastern Arabia	28	15	57 %
ALL ARABIA	147	39	27 %

Source: LARSEN, in press. Many non-migratory species found in Yemen will be recorded in the Asir eventually. Several migratory butterflies not hitherto

recorded from central and eastern Arabia will eventually be recorded.

It is also to be expected that migratory butterflies are more widely distributed than non-migratory species. Again the pattern in Arabia supports this view (table 3).

Table 3: The proportion of migratory and non-migratory butterflies in different parts of Arabia

Region of Arabia	Proportion of species present	
	Migratory	Non-migratory
All Arabia	100 %	100 %
Yemen Arab Republic	85 %	81 %
Aden District	72 %	59 %
Dhofar	54 %	38 %
Oman	51 %	26 %
Asir	78 %	37 %
Central Arabia	46 %	13 %
Eastern Arabia	41 %	11 %
NUMBER OF SPECIES IN GROUP	39	108 = 147

Migrant butterflies occupy an important place in the total composition of the Arabian butterfly fauna, ranging from about a third to two thirds of the total. This element increases in importance in the inhospitable environments of eastern and central Arabia, not least in oasis habitats. Many of the species can undoubtedly survive for many years without reinforcement, but they are periodically at risk of total extinction in years of excessively harsh environmental conditions. This is true for both tropical and temperate species. Only the specially adapted eremic species and a few hardy tropical and temperate butterflies have a truly permanent foothold.

It is characteristic of many migrant species that they can build up populations with extreme rapidity when conditions permit and this fact probably plays a role in the total survival strategy. Even when migration leads to a great loss in breeding potential from individuals which do not find suitable breeding territories, those that do may be spectacularly successful.

Generally speaking the data from Arabia seem to support the theory of SOUTHWOOD (1962) that migration evolved in hostile environments as an alternative to diapause mechanisms. Migration also allows a population to use temporary occurrence of abundant food supplies in areas where permanent breeding is impossible. An additional advantage may lie in the fact that parasite life cycles are broken up. In May, 1981 I collected 1800 pupae of *Anaphaeis aurota* off one small *Maerua* tree in Oman; I found no evidence of parasitoids in either pupal or larval stage.

It seems that a survival strategy consisting of migration and the ability for

rapid population build-up is a suitable one for colonisation of the extreme arid zones of the Arabian Peninsula. The alternative is very strong specialisation to desert conditions, under low population densities, a feat achieved by very few butterflies.

Abstract

The importance of migration to the butterfly fauna of Arabia. – Notulae Entomologicae.

Migration is of great importance to the composition of the butterfly fauna of the Arabian Peninsula. In the mountains of southwestern Arabia where rainfall is plentiful about 25 percent of the fauna is migratory; this percentage rises to nearly 60 in the arid parts of central and eastern Arabia. This tends to support the hypothesis that migration evolved as a survival mechanism for species living in essentially unstable environments where there is an ever-present risk that the entire population will be eliminated by adverse ecological conditions. The alternative, extremely effective diapausal mechanisms encompassing the ability to remain in quiescense for several years, has been achieved by very few species of the Rhopalocera.

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Über die Ortstreue einiger Tagfalter im Großstadtbereich (Lepidoptera)

von
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Kleinbiotop

Garten, ca. 600 Quadratmeter, Schneebeerhecken, 6 Obstbäume, Steinbeet, Staudenbeet, Strauchgruppen, Rasen. Das Grundstück grenzt unmittelbar an die Peripherie der City der Stadt Rheydt. Es gehört zu einem Stadtteil von einem Quadratkilometer bebautem Gelände, in dem mehr Einzelhäuser als Reihenhäuser die Straßen begrenzen. Außer deren Gärten gibt ein Kirchplatz etwas Luft.

Methode

In der Südwestecke des eingangs erwähnten Gartens steht ein Buddleiastrauch mit dunkelviolettroten Blütenrispen, der über 3 Meter hoch gewachsen ist. Die Buddleia heißt im Volksmund auch Sommerflieder oder Schmetterlingsstrauch. Hunderte von Blüten öffnen sich und verblühen nach einigen Tagen wieder. Ihr Duft ist so intensiv, daß er einige Schmetterlingsarten, darunter echte Wanderfalter, auf mehrere Kilometer Entfernung anlockt. Unter dieser Buddleia saß ich, je nach Witterung, täglich, nur eine Mittagsstunde ausgenommen, von 10.30 bis 17.30 Uhr in einem leichten Klappsessel. Bewaffnet war ich mit einem kurzen Fangnetz, Notizblock, Bleistift und Taschenschere.

Die Schmetterlinge wurden nicht im landläufigen Sinne gefangen, um getötet oder eingesperrt zu werden. Sie wurden für kürzeste Zeit demobilisiert und flatterten nach weniger als einer Minute wieder lustig davon. Sie wurden genau nach Art und – soweit optisch leicht erkennbar, auch auf das Geschlecht unter-